

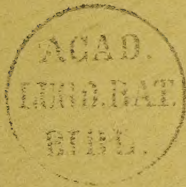
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FOUNDED BY JOHN D. ROCKEFELLER.

A CONTRIBUTION TO THE COMPARATIVE PHYSIOLOGY OF COMPENSATORY MOTIONS.

A DISSERTATION

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BY

ELIAS P. LYON.

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[From the Hull Physiological Laboratory of the University of Chicago.]

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INTRODUCTION.

WHEN a frog is placed upon a horizontal turntable and revolved not too rapidly, the head of the animal turns to one side in the direction opposite to that of revolution. This is an example of compensatory motion. The animal is said to compensate or tend to compensate the passive revolution by trying to keep its head in its original position in space. The head is held in its side-inclined position as long as the revolution is continued. If the turntable is suddenly stopped, the frog moves its head back not only to the normal mid-line of the trunk but beyond, the inclination being now in the direction of the previous revolution. This is an example of "after-effect." After a few seconds the head returns to its normal position.

Pigeons upon being similarly revolved exhibit a bending of the head like that shown by the frog. This motion may amount to 120° , and has been called by Breuer the "reaction movement." Unlike the frog, however, the pigeon does not retain the new position, but with a quick jerk the head is moved suddenly, in the direction of the turntable revolution, part way back to its normal position. This jerk is the "nystagmus phase." Immediately the head begins to move again oppositely to the direction of body revolution, not with a jerk, however, but with slow, steady motion. This is the "reaction phase." After attaining again nearly or quite the maximum angle of the reaction movement, the head

is once more jerked back, and so on, each reaction phase being followed by a nystagmus phase. The result is a series of pendulous motions in a horizontal plane, slow in the direction opposite to that of general revolution, quick in the direction of revolution. The slow reaction movements are compensatory. The nystagmus is a convulsive reflex of secondary character.

If the revolution be long continued, the vibratory motions as a rule become weaker and finally cease. When now the turntable is stopped, the pigeon, like the frog, turns its head in the direction of revolution past the sagittal plane of the body. But unlike the frog, the pigeon's head shows a marked after-nystagmus.

If the head of a pigeon be held during revolution, and in some pigeons regularly without holding, compensation is effected by the eyes instead of by the head. The eyes exhibit the reaction and nystagmus phases in exactly the same manner as does the head. After nystagmus in the opposite direction follows a sudden stoppage of revolution. Rabbits and many other mammals show the same phenomena. The dog-fish (*Mustelus canis*) also compensates rotation about a dorsiventral axis by moving its eyes in the opposite direction. But this motion is accompanied by little or no nystagmus. The eyes are kept in their compensating positions as long as rotation continues. The eyes, furthermore, sometimes show the same motions when the animal moves voluntarily and normally. A dog-fish, for example, when swimming on its side may keep the upper eye to the ventral, the lower one to the dorsal side of the orbit. Compensatory motions are not, therefore, confined to passive rotation by external means.

Mice and many other vertebrates when revolved not too rapidly upon a horizontal turntable run in circles opposite to the direction of revolution. If the turntable moves clockwise, the animals go the reverse. Here compensation is effected by locomotion.

The compensatory motions so far mentioned, whether of the head, eyes, or entire body, tend to keep the same field of vision before the eyes. In few, if any cases, however, do they accomplish this. Even a slow and small rotation, so far as my measurements show, is almost never entirely compensated. If compensation is a device for retaining the field of vision, it does not perfectly accomplish its purpose.

Besides these compensatory motions certain vertebrates upon passive rotation display compensatory motions which seem intended

to return the body to its original position in space. When the dog-fish, for example, is rotated about a longitudinal axis, the fins move in the same direction as the rotation, not opposite to it as do the eyes.

When the animal is rotated in horizontal planes the compensating positions of head, eyes, body, or appendages are retained, or the motions of the same continued only during the rotation. But when the rotation is in vertical planes,—that is, in vertebrates whose chief axis is ordinarily horizontal, rotation about either a longitudinal or a transverse axis,—the compensating positions are retained as long as the animal is held in an unusual position. It is to be noticed that in horizontal rotations the orientation of the animal with respect to the direction of gravity remains unchanged. In rotation in vertical planes the orientation with respect to gravity is changed. In the former case the compensating positions are not retained. In the latter case they are.

The instances of compensatory motions mentioned above are from the works of Breuer, Ewald, v. Cyon, Lee, and others, and are to be considered types of one general phenomenon.

THEORETICAL CONSIDERATIONS.

For the explanation of these motions on the basis of ordinary reflexes three things have seemed to be necessary: (1) a peripheral organ capable of stimulation by gravity, centrifugal force, inertia, or the stresses and pressures resulting therefrom. This organ should be connected by means of nerves with (2) a centre in the brain which should interpret the stimuli received by it from the peripheral organ, and in turn should be connected by means of nerves with (3) the muscles by which the compensatory motion is brought about. The hypothetical peripheral organ or organs have been the *ignis fatuus* of a generation of physiologists. Not content with simple reflexes, they have originated two new senses, the dynamical and statical, and have devised a very complicated theory for their stimulation. So far as facts go, it is pretty generally admitted that cutting of the optic nerves together with sufficient destruction of the inner ear is sufficient to do away with compensatory motions. As to the theory it may be stated in general terms as the view of many physiologists (1) that the semicircular canals are of a "dynamic" character, being stimulated by the active or passive motions of an animal and arousing compensatory motions which continue only during stimulation of the nerves ending in these canals; (2) that the otocyst is a

"static" organ, constantly stimulated by the pull of the stone upon nerve endings and leading to the continuance of compensating positions whenever the body is out of its normal orientation with respect to the vertical. While recognizing the beauty of this theory, and the array of experimental evidence which has been brought forward in its support, the writer has come to doubt the validity of the theory so far as compensatory motions are concerned.

The semicircular canal theory rests first upon the anatomical fact that the canals are arranged in three planes of space approximately at right angles with each other. They seem therefore by this geometrical relation to be organs well adapted to the mediation of movements either in the plane of any one canal or, on the principle of the parallelogram of motions, in any other plane whatsoever. Is this arrangement of canals able to explain all compensatory motions? Professor Loeb calls my attention to the following argument: Suppose a frog is placed upon a horizontal whirling table, so that it faces the periphery of the wheel. In the accompanying figure (Fig. 1), *C* represents the axis of rotation and *A* the position of the animal's head and the horizontal canals. The table is then rotated clockwise or in the direction of the arrow *D*. The animal turns its head to the left in the direction of the arrow *C*. Ac-

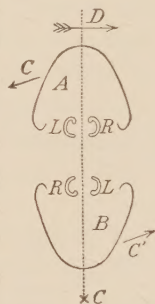


FIGURE 1.

cording to the theory, there is a flow of endolymph from the right canal into its ampulla, or at any rate an increase of pressure in the latter and a flow away from or decrease of pressure in the left ampulla. This difference in liquid pressure or flow acts as a stimulus which arouses the proper chain of internal processes leading to the contraction of muscles and the visible bending of the head. Briefly stated, the theory would assert that stimulation of the right ampulla leads to a bending of the head to the left.

But suppose the animal is so placed upon the turntable as to face the axis. This position is marked *B* in the diagram. Let the turntable be revolved as before. The head bends as before *to the animal's left*, in the direction of the arrow *C'*. According to theory there should be increase of pressure in the ampulla of the side moving in advance, that is the *left*, and decrease of pressure in the *right*, exactly the reverse of the condition when the animal faces outward. *But the same reaction follows.* The animal bends its head to its left.

According to theory, stimulation of the left ampulla should cause the head to be inclined to the right. It does not do so. Therefore the theory is incorrect.

The adherents of the semicircular canal theory were forced to admit its insufficiency in cases where compensatory positions were held after rotation had ceased. They fell back upon the otolith and the "static equilibrium." It seems to me the case cited demonstrates the inability of the theory to account for certain "dynamical" phenomena as well. Cyon and Ewald long ago showed that the canals could be compressed or plugged up without interfering with compensatory motions.

ROTATION EXPERIMENTS.

The types of compensatory motions which I mentioned in the opening of the paper were all found first in vertebrates, animals having semicircular canals. If compensatory motions were confined to this group of animals at least the argument of coincidence would be favorable to the theory. But they are not so confined. Furthermore, if the reactions were found only in animals having otoliths or otocysts, we might with propriety seek a relation of cause and effect. But they are found in animals, having neither semicircular canals nor otocysts. I shall show that every type of compensatory motion found in vertebrates is duplicated in invertebrates; that even the accompanying reflex nystagmus is discernible, demonstrating the unity of the phenomena in both divisions of the animal kingdom; that these reactions occur not only in animals with semicircular canals, but also in those destitute of otocysts; and that therefore the canal-otocyst hypothesis is either entirely incorrect or of merely secondary importance.

Kreidl,¹ in his famous experiment in which he caused Palaemon on moulting to replace its otoliths with metallic iron, seems to have been the first to notice compensating motions of the invertebrate eye. "It is interesting to note," he says, "that in these invertebrate animals also the reflex movement of the eye is present." This seems to have been observed in sidewise inclination only. He found that this crustacean reacts upon the turntable exactly like some vertebrates, running in circles opposite to the direction of rotation.

The animals with which Kreidl experimented are provided with

¹ KREIDL: Sitz.-Ber. der kais. Akad. der Wissensch., Wien, 1893, cii, Abth. 3, p. 149.

otoliths. Is it possible that compensatory motions can be present in crustaceans without otoliths? Indeed it is, for Clark¹ found that *Gelasimus* and *Platyonichus* give very prompt responses upon rotation in vertical planes. And these responses agree point for point with those manifested, for example, by the dogfish, which possesses semicircular canals and otoliths. For instance, on rotating the crabs to the right about a longitudinal (horizontal) axis, the eyes roll to the left, and their new positions are retained as long as the animal is held in an inclined position. Yet Clark's results were looked upon not as contradictory, but confirmatory of the commonly accepted hypothesis.

Gelasimus was revolved on a horizontal turntable and "showed no reaction to slow turning," and when rapidly revolved "no after-effects were observed." Upon turning the crab about its dorsi-ventral (vertical) axis, no compensating movements of the eyestalks were discovered. This, of course, was favorable to the theory, as the animal has no semicircular canals.

After the appearance of Clark's paper, Professor Loeb desired me to perform similar experiments on the crayfish at Wood's Holl. This desire was stimulated by the recollection of certain experiments of his own upon the pelagic gastropod *Pterotrachea*, the results of which were never published. This form is very transparent, and the otocyst, which lies some distance from the central ganglia, can be seen plainly and easily taken out with a hooked needle. Its removal was accompanied by no disturbance of the equilibrium whatsoever, although the animal is very active. It therefore seemed to Professor Loeb that further investigations were necessary before the theory of the equilibrium function of the otocyst should be given universal application or acceptance. This seemed to him the more needful from the fact that insects and other forms possessing no otocysts are yet able to preserve their equilibrium perfectly.

The crayfish.— In order to detect and measure the movements of the eyestalks upon rotating the crayfish around a longitudinal axis, the apparatus shown in Figure 2 was devised. It will be referred to as Apparatus A.

To the base (*a*) are fastened the uprights which carry the rotating board (*b*). This board can be turned by the crank (*f*) into any desired position and held there by the spring-brake (*g*). The amount of turning of the board and consequently of the animal

¹ CLARK: Journal of physiology, 1896, xix, p. 327.

is read from the graduated circle upon the upright (*c*). The animal is fastened to the rotating board by means of rubber bands. The

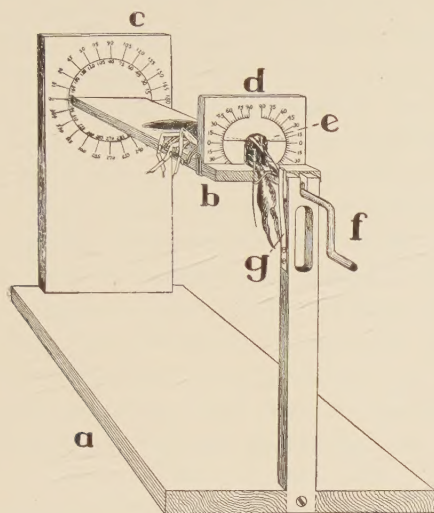


FIGURE 2.

block (*d*) is notched so as to fit over the animal just back of the eyes, and is fastened in this position by a rubber band extending under (*b*) as shown in the figure. To this upright block is attached the mirror (*e*) carrying arcs of graduated circles whose centres are at the bases of the eyestalks, and therefore in the axis of rotation of the latter. It was found that light indicators could be glued to the eyestalks without interfering with their motions. Bristles were generally used for this purpose. These indicators extended before the mirror and slightly beyond the edge of the

graduated circles. By this device errors of parallax were avoided, and motions of the eyes of one degree or less could be detected.

In the following experiments the words "left" and "right" will refer to the animal's left and right.

Rotation in a transverse plane, i. e. about a longitudinal axis.—The turning of the eyestalks of the crayfish upon rotation of the animal about a longitudinal axis has been mentioned by Clark. He did not, however, make a study of it. Just as in other crustaceans studied by him and in various vertebrates described by several observers, the eyes of the crayfish tend to keep their positions in space when the animal is turned in transverse planes. This tendency leads to a movement of the eyes (with reference to a point on the animal) opposite in direction to the motion of the animal itself.

If the animal is stopped at any point in an arc of 180° from its normal horizontal position, the eyes retain the position into which they have come during the rotation. The details of the reaction will now be described.

Normal animals were placed in Apparatus A. So long as the animals remained in their usual horizontal position, the eyestalks were held at an angle of 18° to 25° above the horizontal. Turning

an animal towards its right up to nearly 90° is accompanied by an approximately proportional movement of the eyes towards the animal's left. This movement of the eyes, although proportional to the amount of rotation, is at no part of the arc equal to it. In other words, the eyes do not keep their positions in space but only "tend" to do so. The two eyes do not move through equal arcs. Rotation through 90° towards the animal's right is accompanied by a movement of the right eye towards the left (or dorsally) of about 35° , and of the left eye towards the left (or ventrally) of about 25° .

If the rotation be continued beyond 90° , the movement of the eye-stalks continues. It is, however, no longer proportional to that of the animal, but becomes less and less for each increment of rotation. After rotation towards the right through 120° the left eyestalk becomes stationary at about -10° on the mirror scale, having moved about 30° . Continuing the rotation to 150° the right eye also becomes stationary at about 60° to 65° , having moved in all over 40° .

The eyes make no further movements until the animal has been turned through about 200° from its original horizontal position, when they begin to move in the same direction as the animal, in other words, back towards their normal position. The movement is irregular and may continue after the animal has come to rest in any position between 200° and 300° , but the eyes never come back to the position they would have occupied had the animal been rotated in the opposite direction to the same point.

At about 320° the eyestalks again begin to turn in a direction opposite to that of the animal; and at 360° , the animal having made a complete rotation, the right eye is a few degrees above, and the left eye a few degrees below, the normal position.

These movements are represented graphically in Fig. 3. The abscissas show degrees of rotation of the animal towards the right. The ordinates show the position of the eyes on the mirror scale. The continuous curve represents the motion of the right eye with reference to the line connecting the bases of the eyes. The dotted line represents the motion of the left eye in similar manner. An upward movement of the locus indicates motion of the eye dorsally; downward movement, motion ventrally.

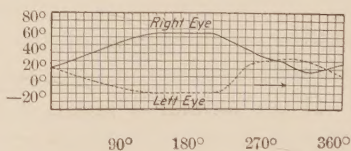


FIGURE 3. The turning of the eyes of crayfish for rotation through 360° to animal's right.

In the case of the right eye, therefore, an upward movement of the locus denotes turning in a direction opposite to that of the animal. In the case of the left eye, the reverse is true. If the animal were rotated towards its left, the motions of the eyes and their resulting loci would be reversed.

The amount of eye motion for a given arc of rotation, say 90° , varied with the quickness of rotation. If the animal was rotated slowly, and especially if it was stopped several times in the arc, the turning of the eye corresponding to 90° of rotation was larger by 5° or more than when the animal was rotated quickly.

Compared with Clark's results on *Gelasimus* the following differences are observed on turning crayfish around an antero-posterior axis: (a) less movement of eyes; (b) continuation of motion of eyes when animal is rotated beyond 90° ; (c) upon rotation beyond 180° the eyes never take the positions they would have had if the animal had been brought by opposite rotation into the same position.

To test crayfish for after-effects, normal animals were quickly rotated ten times about a longitudinal axis. No after-effects were ever observed.

Rotation around a transverse axis. — Just as Clark found in *Gelasimus*, the crayfish upon being turned forward around a transverse axis moves its eyestalks backwards; and, upon being turned backwards, turned its eyes forwards. As there seemed to be nothing particularly different in these motions from those already described, they were not extensively studied.

Rotation about a vertical axis. Nystagmus. — Early in my work I found that, contrary to Clark's assertion for *Gelasimus*, the crayfish clearly showed compensatory motions of the eyes on rotation in horizontal planes about a dorsi-ventral axis. As such a reaction had never been reported, I studied it in some detail, and devised a modification of Apparatus A for that purpose.

The animal was fastened by means of rubber bands to a piece of flat wood. At each side of the head a small piece of board about 1.5 cm. thick was fastened in such a way as to bring small horizontally placed mirrors bearing graduated quadrants of circles a few millimetres below the eyestalks. The bristles fastened to the eyestalks extended over these mirrors. The animal was rotated either by hand or by the kymograph, the holder resting on the top of the drum.

The eyestalks are normally held at angles of 65° to 80° with the median, dorsi-ventral plane. When the animal is rotated around a

vertical axis they move 10° to 18° in the opposite direction. For the first few degrees of rotation the eyes seem to retain their position in space absolutely, *e. g.* if the animal was moved through 5° towards its right, the eyes moved 5° towards the animal's left. In this respect the rotation in a horizontal plane is different from that in a vertical plane, in which the movement of the eyes is for a time proportional to, but at no part of the arc equal to, the angular motion of the animal. Beyond 5° , however, the eyes did not keep pace with the angular motion of the animal.

When the eyes had moved 10° to 18° as indicated, they became stationary, and then with a quick jerk moved 3° to 5° towards their original position. Both eyes moved at the same instant and through the same angle. If the rotation of the animal was continued, these oscillatory motions of the eyes were repeated at fairly regular intervals for some time. After several rotations, however, they became fewer and finally ceased.

Using Breuer's nomenclature, the eyestalks of the crayfish show, therefore, a "reaction movement" through 10° to 18° , a "nystagmus phase" of 3° to 5° .

Upon bringing the animal into a condition of rest no after-effects of any kind were observed.

The nystagmus effects were the same when the animal's field of vision was made to rotate with it by surrounding it with a pasteboard cylinder. I should, however, state that a space was left at the top for observing the animal, and therefore the experiment was perhaps incomplete. After rotating the animal for a time in one direction, reversal of the motion made the nystagmus more frequent and regular.

No facilities were at hand for observing the animal under rapid rotation. Within the limits of velocity in which the eyes were directly observable, the effects were always found. They were most favorably seen when the rotations numbered two or three per minute. Under such circumstances there were seven to ten nystagmus movements per rotation. I was so much surprised and impressed with these results that at Woods Holl last summer I repeated the experiment on Clark's animals, *Gelasimus* and *Platyonichus*, as well as several other crabs and the lobster. In no instance did I fail to find compensatory motions of the eyes upon rotation about a dorso-ventral axis. In *Gelasimus*, the nystagmus is especially marked and frequent. The demonstration needed no apparatus whatsoever, and never failed in dozens of individuals examined.

Experiments with the horizontal turntable. — Like Miss Bunting,¹ I was unable to detect in large crayfish any inclination to rotatory locomotion when they were revolved on a horizontal turning table. On the contrary, Kreidl reports a very prompt reaction in *Palaemon*. And upon experimenting with small crayfish about 2–3 cm. long, I was surprised to find a very lively reaction to the turning table. The animals moved in small circles opposite to the direction of revolution. It was not an effort on the part of the animal to keep as far as possible from the observer. At Wood's Holl I tried *Gelasimus*, and found that these and other crabs show the same reaction. When revolved towards the right, they run in circles to the left just like a mouse or salamander.

Insects. — Dr. Loeb² has called attention to the fact that certain insects experimented upon by him, *e.g.* houseflies and beetles, react to revolution on a horizontal turntable. They behave exactly like vertebrates, running in circles opposite to the motion of the turntable. Here then is a very definite compensatory motion effected by animals not only without semicircular canals but also devoid of otocysts. K. L. Schaefer³ later revolved crabs, earthworms, caterpillars, various insects, and snails, and claimed that only the latter gave any response. Upon further study of the insects, however, I have been able to establish in them almost every type of compensatory motion which has been described in vertebrates. In all the following experiments it will be understood that imagoes were used.

A large beekiller (*Asilus*) was slowly revolved upon a horizontal turntable and showed very prompt reaction of the kind described by Dr. Loeb. When it was rapidly revolved, there was no after-effect. The same reaction upon revolution and the same lack of after-effect was manifested by locusts, grasshoppers, dragonflies, several species of flies, ants both red and black, and several forms of beetles. The phenomena would appear therefore to be very common if not of universal occurrence among adult insects.

The potato beetle reacts to the turntable like the other insects, but shows an interesting pseudo after-effect. If the revolution be sud-

¹ BUNTING, M.: Archiv f. d. ges. Physiol., 1893, liv, p. 531.

² LOEB, J.: Der Heliotropismus der Thiere, etc.; Anhang, Einige weitere Versuche über den Geotropismus der Insekten, Würzburg, Georg Hertz, 1890.

³ SCHAEFER: Naturwissenschaftliche Wochenschrift, Nov. 25, 1891; also Zeitschrift für Psychologie und Physiologie der Sinnesorgane, 1892, iii, 2 and 3.

denly stopped, the animal does not cease its circular motion instantly, but continues for an observable interval to move in the same direction as during revolution, *i. e.* opposite circles. After a moment it starts off in a straight line. If this were a true after-effect it would be in the opposite sense to those after-effects seen in vertebrates, which are always in the same direction as the revolution. In the case of this beetle it must be considered, I think, as a sort of "personal equation," an interval between the cessation of the stimulus and the cessation of muscular response. If the beetle is crawling across the turntable and the table is started with a quick jerk through a partial revolution and immediately stopped, the beetle may be found still moving in a straight line. In an instant, the turntable being now at rest, the beetle makes a partial circle opposite to the previous motion of the turntable and then starts off again in a straight line. Almost a second must elapse between the stimulus, whatever it may be, and the corresponding compensatory motion — much too long a time for the latter to be of any benefit to the animal.

Nystagmus. — The head of the beekiller is connected to the thorax by a very slender "neck" and is therefore extremely mobile. When the animals were held in the fingers and rotated about a dorsi-ventral (vertical) axis, the head made characteristic compensatory motions accompanied by nystagmus. Every phase was as clear as in the pigeon. The slow and steady "reaction phase" and the quick and jerky "nystagmus phase" were beautifully distinct. No apparatus or training is necessary to demonstrate this fact. Dragonflies display the same in less marked degree.

Sustained compensatory positions. — When the beekiller is rotated about a transverse (horizontal) axis, the head makes compensatory motions unaccompanied by nystagmus. For example, when the animal is tipped forwards, anterior end downwards, the head moves dorsally, *i. e.* opposite to the motion of the animal. This reaction also is very marked. The proboscis in the normal horizontal position of the body is directed ventrally at right angles to the body axis. But when the animal has been turned forwards through 90° , the proboscis points almost in the longitudinal axis. When turned head upward the opposite occurs; the head moves ventrally and the proboscis comes to lie close against the thorax. *In both of these cases the compensating position is retained so long as the body is held in its new orientation with respect to the vertical.* No one has found an otocyst in the beekiller.

No well marked compensatory motions were seen upon rotating these animals about a longitudinal axis. A twisting of the head, such as the pigeon exhibits, was perhaps to be expected. But I have made no observations as to whether the beekillers are accustomed normally and voluntarily to make such a motion. If not, it would hardly be expected as a reflex.

OPERATIVE EXPERIMENTS ON THE SEMICIRCULAR CANALS AND OTOLITHS.

I owe to Dr. Loeb the ingenious suggestion that Nature has worked out in the flounder the solution of the semicircular canal problem. As is well known, this fish when hatched, and for a considerable time thereafter, is as symmetrical as any vertebrate and has an eye upon each side of the head. Later it gradually turns upon one side and finally becomes quite asymmetrical. The eye of the lower side comes to the upper side, the change being accompanied by marked alteration of the bones of the head; the two sides become different in color and shape; the mouth also gradually loses more or less of its symmetry.

Dissection shows, however, that no shifting has taken place in the brain or in the ear. The transverse axis of the brain, therefore, is now vertical. The morphologically horizontal (external) canals are also vertical; the morphologically vertical canals lie in planes half way between the horizontal and vertical; the stress relations of the otoliths are entirely changed. It would seem, therefore, that here is an animal especially suitable for testing the supposed dynamical and statical functions of these organs. Furthermore the animals are very hardy. Artificial respiration can easily be maintained for an indefinite period. The semicircular canals, though not so easily accessible as those in the cartilaginous cranium of the dogfish, can be laid bare without undue difficulty or delay and with practically no bleeding. In a fair sized fish they are a centimetre or more in length, and therefore of sufficient size to make the operator sure of what he is doing.

The fish used in these experiments was *Pseudopleurinctes Americanus*, the common "winter flounder" occurring at Wood's Holl. It lies upon the right side; the eyes therefore are both upon the upper, left side. Though a bottom fish, it is quite active. If turned "wrong side up" in the water it immediately recovers its normal position without preliminary contact with solid bodies. *The compensatory motions of the eyes are exactly like those of other fish.* Compensatory positions corresponding to changes of orientation with respect to the

direction of gravity are sustained so long as the body is held in its abnormal position. Morphological relations are entirely subsidiary. If the animal be turned in vertical planes the eyes move in the opposite direction in the same planes. Therefore if the canal theory be true, the morphologically horizontal canals are now mediating motion in vertical planes. Considering the asymmetrical position of the right eye this result seems quite wonderful. It is possible that the muscles of this eye have also so shifted that its present motion, which is opposite of course to its original motion when on the right side of the fish's body, is accomplished by the same muscle or set of muscles as before. On the other hand, if the shifting of the eye is unaccompanied by such rotation, the canal theory would demand a considerable shifting of nerve connections. I have not been able either to determine the matter by dissections or to search the anatomical literature for its possible demonstration.

Throughout my experimental work I have tried to adhere to the following rules: —

1. If stimulation of a sense organ or part of the nervous system calls forth a certain reaction (motion) it is certain that the stimulated organ is connected by nerves with the centre of this motion, but not that the stimulated organ is itself the centre.

2. If through extirpation of an organ a function is eliminated, it is certain that the extirpated organ is connected by nerves with the centre of this function, but not that it is itself the centre.

3. If after extirpation of an organ a function which ordinarily is lost after this extirpation remains *in one case only*, it is certain that the extirpated organ is not the sole centre of this function.

Bearing in mind the third principle in particular I have tried to give attention to the exceptional cases instead of throwing them out altogether, as is too often the custom, and founding conclusions upon the basis of majorities. This method, one can readily see, demands constant care. The exceptional case of a function retained after removal of an organ whose loss ordinarily entails obliteration of that function may mean nothing more than an imperfect operation, the residue of an organ or a partially severed nerve. It is but fair to state that I have borne these considerations in mind, and that if errors have crept in, they are not attributable to want of conscientious care. Post mortem examinations were always held, and were generally witnessed by Dr. Loeb or Dr. Norman. I might also add that I began these experiments a believer in the otolith-canal theory.

Extirpation of canals. — *The flounder.* — The (morphologically) vertical canals anterior and posterior were removed from both sides. The nerve leading to each ampulla was first cut and the canal and ampulla removed together. Immediately after the operation the animal was revolved about a longitudinal axis and showed normal compensatory motions. Yet all the canals which should mediate such motion had been removed. Revolved about a dorsi-ventral (horizontal) axis, there was little or no compensation. Yet the canals in the plane of this motion were still intact. The slightest stimulation of these (morphologically horizontal) canals still gave strong and perfectly definite motion of the eyes in the plane of the canals. This happened in two animals. These animals were very strong and vigorous. The eyes reacted to touch after the operation and little evidence of shock could be detected.

Remember that there cannot be the slightest doubt as to which canals were removed or as to their entire removal. Yet compensatory motions remained in the plane of the extirpated canals and were largely lost in the plane of the remaining canals, while stimulation of the latter still gave rise to the motion of the eyes in the plane of these canals. It appeared certain to those who saw these animals that there could not be any stimulation of the horizontal canals without motion of the eyes. Yet no motion of the eyes followed rotation in the plane of these canals. The conclusion was irresistible that rotation of the animal did not stimulate the horizontal canals. The compensatory motion seen in normal animals on rotation in this plane must arise from some other source.

In one individual all six canals and ampullæ were entirely removed, and yet a large amount of compensatory motion on rotation about a longitudinal axis remained. It was perhaps a little less than normal. At the same time a small amount could be detected on rotation about a dorsi-ventral axis. My notes say : "Is very lively, eyes held far out, not drawn in at all." And this leads to the remark that it was the strongest animals and the cleanest, quickest operations that gave these results. While in many cases one would find after the operation little or no compensatory motion, yet at the same time evidences of severe shock were observable. Often the eyes showed no reaction to touch and appeared sunken in their orbits. Indeed, toward the last I came to know that if the eyes would not react to touch, there was sure to be no response on rotation. This was more common in the dogfish than in the flounder. It was the strongest, least injured

animals which — from the standpoint of the canal theory — gave the worst results!

The dogfish.—Two specimens of *Mustelus canis* from which all the ampullæ were entirely removed gave results very like the above. I quote from my notes:—

Case I.—“Small lively dogfish. All ampullæ of both ears removed. Animal very lively after operation. Eyes react to touch. Placed in aquarium, gives regular compensatory motions on rotation about transverse axis, almost as great in degree as normal. Can detect nothing on other rotations. Eyes appear normal; are moved a good deal but in no constant way. *Next day.* Animal still very lively. *Never turns on back.* Makes what are perhaps horizontal circus motions when disturbed [*i. e.* swims round and round in the aquarium], but to either right or left; seems rather trying to escape than subject to forced motions. Motions seem perfectly co-ordinated. Animal stopped with head up against side of aquarium; eyes compensated properly, *i. e.* rotated anterior end ventrally, posterior end dorsally. Animal came to rest next minute in horizontal position; eyes also horizontal. Rotated slowly about either a transverse or dorsi-ventral axis accompanied by nearly perfect compensatory motions. About longitudinal axis, compensatory motion of fins perfect. Turned on back by hand, resists and quickly turns back.”

Case II.—“Medium sized dogfish. On right side—cut nerve of (1) anterior vertical canal, (2) posterior vertical, (3) horizontal canal; on left side—(1), (2), and (3) successively. Operation very free from blood. Everything visible. Immediately after operation, no reaction. Animal in shock, and eyes show no spontaneous motion when first put in aquarium. After half an hour is much revived. Eyes make spontaneous motions little different from normal. Perhaps irregular nystagmus. [But the normal dogfish often moves its eyes rapidly and irregularly.] On rotation in vertical planes about a longitudinal axis compensatory motions of eyes indistinguishable from normal. Pectoral fins show marked compensatory motion. Dorsal fin appears to move slightly. Body stiff; almost impossible to bend; is kept bent concave to left. Rotation from horizontal to head up about transverse axis, left eye rotates very markedly in opposite direction. Right eye slightly.”

In all these animals, both flounders and dogfish, it will be objected that the otolith was still intact and that the sense of sight remained unimpaired. Both objections are well founded so far as they express the anatomical condition of the animals. If it be true, as v. Cyon¹ quotes from Beer, that the dogfish is day-blind, the latter objection would lose much of its force, but Beer's statement is contradicted by

¹ VON CYON: Archiv für Physiologie, 1897, p. 77.

Lee,¹ with reason as it seems to me, for dogfish swimming in a large pool appear to see well. It has never been claimed that the otolith could effect compensatory motions on rotation in horizontal planes. Such motions were clearly exhibited by the dogfish, mentioned as Case I, which had lost all its canals and ampullæ.

Stimulation of canals. — If the theory of the semicircular canals is an expression of fact, stimulation of any canal should lead to motion of the eyes in the plane of that canal. Since the time of Flourens, many physiologists have made this assertion until it has become recognized as a well-established physiological fact. Yet in the flounder and dogfish, at least, it is but partially true. Furthermore it would be expected, as Professor Loeb pointed out to me, that if there were any difference in the irritability of the canals, it should be in favor of the vertical canals. For rotation of a fish in vertical planes is followed by a larger motion of the eye than rotation in horizontal planes. This supposition also is not true. When I began work on the flounder I had no idea that the canals were different in sensitiveness or that motion of the eyes in the plane of one canal upon stimulation of that canal would be more difficult of demonstration than in the plane of another canal. When, however, I came to compare the results of the first few operations, it was noticeable that *stimulation of the (morphologically) horizontal canals never failed to call forth motion of the eyes in the plane of the canal, while stimulation of the vertical canals either gave no results or motions of an indefinite character.*

Even with a mind at that time favorable to the theory, stimulation of the vertical canals in these first experiments gave me nothing better than—to quote from my notes: “Slight motion of eyes, seemingly in plane of canal;” “About 30° from plane of canal;” etc. Most often the notes read: “Not clear,” “Indefinite,” “No results,” “Rotation not in plane of canal,” etc.

As soon as I had grasped the significance of the difference between the horizontal and vertical canals, I began a series of experiments to ascertain whether the differences so far observed were individual or universal. The canals were exposed in different sequence, sometimes beginning with the anterior vertical, sometimes with the posterior vertical, sometimes with the horizontal. Different means of stimulation—a blunt needle, a tuft of cotton, a weak electric current—were employed. The results were indubitable. The morphologically

¹ LEE, F. S.: This journal, 1898, i, p. 136.

horizontal canals of the flounder are much more sensitive, measured by the resulting compensatory motions, than the vertical canals. Stimulation of the vertical canals near the ampullæ often gave no results whatever; while the slightest touch upon the horizontal canal, even far from its ampulla, led to prompt and very marked motion of the eyes in the plane of the canal. Even through a layer of bone a slight pressure over the horizontal canal found instant response in motion of the eye in the plane of the canal. While working near the vertical canals one perceived far more eye-motion in the plane of the horizontal canals than in that of the canal which was being uncovered. Stimulation of the vertical canals seldom or never gave responses in the planes of the canals. On the other hand the stimulation of the horizontal canal always produced motion of the eyes in the plane of that canal.

A few experiments upon dogfish convinced me that the same is true there. The horizontal canals are much more irritable than the vertical canals. Stimulation of the horizontal canals leads to definite motion of the eyes in their plane. Stimulation of the vertical canals gives very indefinite and indifferent results.

Have not the authors who assert that each canal mediates motions in its own plane founded their claims chiefly upon observations on one canal alone, the horizontal? Have not the vertical canals given them many negative results? Probably if the horizontals were no more sensitive and gave no more definite results than the vertical canals, no one would ever have heard that stimulation of a semicircular canal causes motion of the eyes or head in the plane of that canal.

Extirpation of the otolith in the flounder. — The flounder should be the classical animal for this operation, because the otolith in this fish is a hemispherical body, very firm and massive, and about 1 cm. in diameter. It lies in a capsule entirely apart from the semicircular canals, and can be removed unbroken without the letting of a drop of blood. As is well known, the otolith plays an indispensable part in the equilibrium theory of the ear. Upon the changed stress relations of the stone should depend the retaining of compensatory positions when the orientation of an animal with respect to gravity is changed. An animal from which the otoliths had been entirely removed might be able, according to theory, to make a compensatory motion upon rotation in vertical planes provided the vertical canals remained intact, but it could not on being stopped in any ab-

normal position preserve the compensating organ in the position into which it had come during rotation. *Flounders from which both otoliths had been entirely removed showed persisting compensatory motions* upon rotation in vertical planes about either a dorsi-ventral or longitudinal axis. These motions were very plain, though sometimes a little more slow than normally. The compensating positions were retained so long as the fish was held in an abnormal position. To make sure that sight impressions had nothing to do with this, the optic nerves were cut in an individual from which the otoliths had already been removed. This operation is very easy, as the nerves are several centimetres long and easily accessible. After the severing of these nerves the compensatory motions were as clear and persisting as before.

Professor Loeb¹ several years ago instituted investigations on the otolith of the dogfish. He found that when he washed out the otoliths no disturbance followed. But if the otoliths were scratched out, marked disturbances of compensatory motions resulted. He concluded that in his first experiment parts of the loosely segregated calcareous material were left in the ear and were able to functionate. The experiments on the flounder, on the contrary, where the entire stone can indubitably be removed, make it probable that Professor Loeb's washing experiment was the better of the two, and that his results were against, rather than favorable to, the otolith hypothesis.

Extirpation of the otocyst in crustaceans. — The antennules of the crayfish were removed by means of small scissors. In each case a microscopical examination was made to determine whether the organ was entirely extirpated. In the latter part of the investigation it was found that the animal sustained the loss of the rostrum without inconvenience. By performing this operation a few days before removing the otocysts, the latter operation was made easier and surer.

The removal of one antennule led to a lessening of the compensatory motions of the eyes on rotation in vertical planes. There seemed to be, however, no constant difference in the two eyes in this regard. Few experiments were made.

The loss of both antennules was the subject of more extensive experiments. The compensatory motions on rotation in vertical planes were always lessened *but never entirely done away with*. The residue was measured by rotating the operated animals in Apparatus A,

¹ LOEB, J.: Archiv f. d. ges. Physiol., 1891, xlix, p. 175.

and varied greatly, being sometimes no more than 8 per cent and again as much as 50 per cent of the original amount. The amount of residual compensation increased for some days after the operation, but at length became stationary, and did not change again although some of the animals were kept nearly a year and moulted one or more times. No regeneration of the antennules took place.

The turning of the eyes in the animals deprived of otoliths was less regular than in normal individuals. Upon motion of the animal through a certain arc and return backward to the starting point the eyes did not return so exactly to their original position. Sometimes rotation in one direction would produce marked movement of the eyes, while the reverse would hardly produce any reaction. This fact I never have been able to explain, but it seems contradictory to the supposition that the residue of compensatory motion after removal of the otoliths is a visual phenomenon and perhaps points to a one-sided loss of muscular energy or to one-sided nerve injury.

The compensatory motion of the eyes and accompanying nystagmus on rotation about a dorso-ventral (vertical) axis were not lessened in animals from which the otoliths had been removed. The same was true of *Gelasimus* and other sea-crabs upon which the same operation had been performed.

Animals from which the otocysts had been removed showed a diminution of general activity. They were not aggressive, and when they did grasp anything with their chelæ, held on less tenaciously than normal individuals.

In this connection I may say that Kreidl's beautiful experiments in which *Palæmon* on moulting was made to place otoliths of fine iron in the cyst and forthwith became susceptible to an electro-magnet as well as to gravitation, have seemed to me the most important proof of the connection of the otolith with equilibrium. Since I began to doubt the theory, I have attempted twice to repeat his experiments, but so far without success. I was unable to catch *Palæmon* at the moment of moulting. I watched them nearly all night, but while those captured late in the evening were often half moulted, they refused to continue the process, or else were unable to do so in the smooth glass dishes in which I had placed them. Some I supplied with eel-grass, with no better result. With small crayfish I was more successful. I saw them take the powdered lodestone with which I supplied them and place it upon the bases of their antennules. In a preliminary trial they did not respond to a magnet. Unfortunately

a thoughtless student placed the animals with some large crayfish, and they were devoured before I had opportunity either to finish the experiment or make a microscopical examination of the cysts.

EXPERIMENTS ON THE EYES.

From the foregoing experiments and discussion it seems certain that the otolith and semicircular canals are not the only organs for the mediation of compensatory motions. The fact that such motions exist in insects is sufficient proof of this point. Either the motions have not in all classes of animals one common cause, or else the semicircular canal and otolith theory is false. It is worth while at least to search for a common organ. Sight is a common function of all animals in which compensatory motions have been observed, and the eyes are perhaps the commonest organs exhibiting these motions. Do all or any compensatory motions arise from stimuli reaching the brain along the optic nerves?

Von Cyon¹ has stated that a frog when its head is covered with a leather cap ceases to display compensatory motions upon rotation on a horizontal turntable. He thinks that many of the equilibrium phenomena which the Mach-Breuer adherents have localized in the ear are really aroused through impressions upon the retina. Others who have worked on compensatory motions have claimed their total cessation when in addition to destruction of the labyrinth the animal was blinded, thus admitting that a part at least of such motions was attributable to the organs of sight. Clark asserts the same in regard to *Gelasimus*, all compensatory motions disappearing when, in addition to loss of the otocysts, sight was eliminated by painting the eyes with lampblack and shellac. He says also that when the eyes of normal crabs were painted, the otocyst being intact, little or no diminution of compensation followed. Lee² found that the compensatory motions of the dogfish were not affected by extirpation of the eyeballs.

Cutting the optic nerves of dogfish and flounders.—The optic nerves of dogfish and flounders were severed. No marked change in the compensatory motions in any plane could be detected. There was perhaps slightly less tendency to retain compensatory positions on rotation in vertical planes.

In the dogfish this operation is accomplished without loss of

¹ VON CYON: *Archiv für Physiologie*, 1897, p. 65.

² LEE: *This journal*, 1898, i, p. 133.

blood or disturbance either of the brain or orbit. The animal is placed upon its back and held down with netting and cords. Artificial respiration is easily established by keeping water flowing through the gills; the mouth is held open; the optic nerves are easily accessible through the skin and cartilage of the roof of the mouth. In the flounder also, as has already been stated, the long optic nerves allow of cutting without injury to the brain or interference with the muscles of the eye or with other nerves.

Crustaceans. — *Loss of sight.* — The eyes were painted two or more coats with a mixture of shellac varnish, and lampblack. Crayfish thus treated always showed a diminution of compensatory motions on rotation in vertical planes, amounting to 10 per cent or more of the total. The loss was, however, never excessive.

The compensatory motion and nystagmus of the eyestalks of crayfish on rotation about a dorsi-ventral axis were not affected by loss of sight. In *Gelasimus*, on the contrary, the same reaction was entirely done away with after the eyes were painted. In crayfish from which the otocysts had been removed, and whose eyes in addition had been painted, very little compensatory motion remained on rotation in vertical planes. *Yet in every case a small amount could be detected*, — one to five degrees.

Effect of light upon compensatory motions. — From the foregoing paragraph it appears that in the light the compensatory motions of a crayfish must be greater than in the dark. Is this effect indirect, the larger eye motion in the light being merely an increased effort to retain a moving retinal impression? Or does the light in some way affect the motion itself? I made a good many experiments to try to answer these questions, and while they have perhaps little bearing on the broad subject of equilibrium phenomena, they may be allowable in an article which attempts to deal only with compensatory motions.

Effect of moving objects upon eye motions. — A cylinder of white cardboard was fitted over the board carrying the animal in Apparatus A so that it could be revolved about the same axis. This cylinder was painted with longitudinal stripes inside, and well illuminated by placing the open back toward a window. When the cylinder was revolved about the animal, the latter being at rest, the eyes followed the motion of the stripes, but never to any great extent. If, for example, the cylinder was revolved 90° , the motion of the eyestalks was only a small part of what it would have been had the animal itself been rotated through the same arc.

This experiment makes it clear that moving objects may influence the eye motions of crustaceans. Other experiments, however, convinced me that light itself can influence the amount of response, and that the different wave-lengths have not equal value in producing this effect.

Effect of light and darkness.—Apparatus A was covered by a wooden box blackened inside. The box was open in front to allow observation of the mirror scales, but projected well forward of the animal, and shut out nearly all light from the animal's eyes. A normal individual which upon rotation from 120° right to 120° left showed in the light a total eye movement of 63° , in the dark box moved the eyes only 51° . The usual difference found was 5° to 8° , always in favor of the light.

Differences could be detected in the amount of eye motion in dark and light portions of the room, and between that on bright and that on foggy days.

Effect of colors.—In another series of experiments Apparatus A was surrounded by a blackened box which projected well in front of the animal but was open for a space of 8 cm. around the animal's head. This space could be filled with glass of any color or covered with black cloth. Animals rotated in this box with the space open showed the same eye movements as in the open room; with space covered with opaque black cloth, the same as in the dark box just described; with space covered with blue glass, nearly and in some instances quite as great rotation as in the open room; with space covered with red glass, usually slightly greater rotation than in the dark but not so great as in the blue light. These effects were the same, no matter in what order the colors were used, provided a slight interval was allowed between the trials. Some of the results obtained were as follows:—

Animal No.	Animal rotated	Total rotation of eyes (average).			
		Daylight.	Blue.	Red.	Dark.
		degrees	degrees	degrees	degrees
43 . . .	From 120° R to 120° L	56.5	55	52	47
45 . . .	" 90° R to 90° L	37.5	35	28.5	29.5
48 . . .	" 120° R to 120° L	52.5	52.5	51	46
49 . . .	" 120° R to 120° L	53.5	51.5	45.5	43.5

The red glass used was for my eye much brighter than the blue.

Effect of light on position of eyestalks.—A normal animal was placed horizontally in the apparatus. The mirror scale and indicators were adjusted. The animal was so placed that the light from a window fell upon the left eye. Upon interposing an opaque object between this eye and the source of light, the eye moved 1° to $2\frac{1}{2}^{\circ}$ towards the vertical. Upon removing the screen, it fell to its former position. Upon interposing a piece of red glass the eye behaved in the same manner as if an opaque object had been used, though the movement was in a few cases less. Using blue glass, there was usually no change in the position of the eyes, either on placing it before the eye or taking it away. Sometimes motions were detected, but they were not so great as those from red glass. In general the blue light acted like daylight, the red like an opaque body. That these effects were not the result of the eye's following the objects moving before it was shown in several ways. (a) If the opaque object be moved horizontally the vertical motion of the eye occurs, being, as already stated, upwards when the light is intercepted, and downwards when it is allowed to fall again upon the eye. (b) If a black card well illuminated on the side toward the animal be moved slowly up past the eye, the latter also moves up gradually as much as 5° or 6° . As soon as the card has passed so that the window light falls upon the eye, it drops back again 1° to 3° . If the black card be moved slowly downwards between the eye and the light, the eye may move down 1° to 2° , but instead of springing back when the card has passed by, the light adds its effect and it falls still farther. (c) If an iris diaphragm is used to shut off and admit the light, the effects are not different than with the simple cardboard screen.

In only two cases was the eye opposite the light seen to move. In these instances this eye moved downwards when the light was shut off, and upwards when the light was readmitted. This experiment did not succeed with all animals. About one specimen in four showed no change on interposing the black card.

This experiment seems to me of some importance, in connection with the theory of heliotropism. To account for the orientation of animals in a ray of light, Professor Loeb¹ has advanced the idea that the tension of the muscles is directly or indirectly affected by light. If, for example, an animal has one side directed to the source

¹ LOEB, J.: *Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen*, Würzburg, 1890.

of illumination, and we imagine that light weakens the tension of the muscles on this side or increases the activity of the unlighted side, it follows that, when the animal moves, it must turn towards the source of light and be positively heliotropic. *The experiment just described seems to show that light may cause such an unequal tension of associated muscles.* When light enters the eye of the crayfish, the eyestalk is not held so high as in the dark. This must be due to inequality in tension of the eye muscles. Either the muscles which lift the eyestalks are weakened, or those which depress it are strengthened, or both are weakened or strengthened in an unequal degree. The effect, too, agreed point by point with the phenomena of heliotropism. The blue rays acted exactly like white light, while red was like darkness or very feeble light.

A further experiment to show that light could affect the amount of geotropic response was made as follows: a half cylinder of cardboard which could be attached to the board carrying the animal and revolved with it was constructed. This covering was painted black inside, and enclosed the animal all around save a lateral slit about four centimetres wide over the animal's eyes and two small holes in front through which the mirror scales could be read. These holes, even, although they were not visible to the animal, were closed during the turning. The only light which reached the eyes came through the semicircular slit in the cylinder, directly over them. The experiments were performed on the roof of the laboratory at a time when the cloudless sky presented a semicircular field of vision of quite uniform illumination and free from objects which might catch the eye. The other half of the field of vision was made as similar as possible by means of mirrors placed beneath the apparatus. The animal on being rotated with the slit open showed, as was to be expected, the same eye motion as if the cylinder were not present. The slit was then covered with a sheet of tissue paper through which considerable light could penetrate but no object could be distinguished. The motion of the eyes for the same rotation of the animal was less. Two and three thicknesses of the paper led successively to lessening of the amount of compensatory motion, the loss each time being 1° to 3° . Removal of the paper layer by layer led to corresponding increases in the compensatory motions.

As in this experiment the animal's field of vision revolved with it, and the only difference was the amount of light admitted by the successive layers of paper, it would seem that light can influence the

amount of compensatory motion independently of the field of vision. And so far as these experiments go, they would indicate that the greater the light, the greater the eye motion for a given rotation of the body.

Under the title *Heterogene Induktion* Noll¹ has collected many instances of the interrelation of stimuli in plants, and has discussed the phenomena at some length. He shows that not every form of irritability can be traced to one, single stimulating cause. For example, he gives the observation of Stahl² that the rhizomes of many plants, as *Adoxa moschatellina* and *Circæa lutetiana*, alter their direction of growth upon being lighted. But strangely enough the phenomena are not of a heliotropic character. Light is not the immediate cause, for on a klinostat the reaction fails. In other words, light is able to influence geotropism. Similarly Schmidt³ found that on the klinostat leaves did not show the so-called heliotropic torsion. He thought that the torsion was due to one-sided over-weight, but Noll says that it is evidently due to a union of heliotropism and geotropism.

It may be that the peculiar relation of the compensatory eye motion in the crayfish to the light is a case among animals of Noll's heterogeneous induction. It surely looks as if the amount of light entering the eye, independent of any visual field, can influence the geotropic response of these animals. I am inclined to believe, however, that the effect of light is a more general one; that in the light the entire animal is tuned, as it were, to a higher key. The tension of the muscles of an animal in the dark seems lower. This shows itself in reflexes and voluntary actions other than the geotropic. Blinded crayfish seem to grasp objects with their chelæ less strongly than usually. Beekillers when blinded rarely exhibit the stabbing reflex. And insects generally live only a comparatively short time after blinding.

Effect of loss of sight on compensatory motions of insects.—The preceding statements lead naturally to the inquiry as to what effect blinding has upon the compensatory motions of insects. I made numerous experiments to settle this point. Houseflies cease to react on the turntable as soon as the eyes are blackened. Placed on

¹ NOLL, F.: Ueber heterogene Induktion, 1892, Leipzig, W. Engelmann.

² STAHL, E.: Berichte der deutschen botanischen Gesellschaft, 1884, ii, p. 383.

³ SCHMIDT, O.: Das Zustandekommen der fixen Lichtlage blattartiger Organe durch Torsion, Inaugural Dissertation, Berlin, 1883.

their backs they would remain there for a long time without making any effort to get up. But they would still crawl up a vertical surface, and if turned head downward showed a strong tendency to reverse their position. The same was true of the locust and potato beetle. This geotropic response has, therefore, nothing to do with the eyes, as was indeed to be inferred from Professor Loeb's¹ experiment in which cockroaches confined in a dark box were found upon the vertical walls and with their anterior ends directed upwards.

All other insects experimented upon were like the housefly, showing no reaction to the turntable after both eyes were painted.² The compensatory motions and nystagmus exhibited by the head of the beekiller also ceased with loss of sight. As a rule, also, insects when blinded show marked loss of equilibrium and often refused to fly or move in a normal manner. The eyes, therefore, in accordance with the supposition of Delage,³ seem to be the most important organs of equilibrium for these animals.

To sum up my experiments on insects, it may be said that while all the species tried showed compensatory motions of one or more forms, these motions ceased entirely when the eyes were thrown out of function. The most natural explanation would be that these motions were roused by the shifting of visual impressions. I am not entirely certain, however, that this is the true, or at any rate I am doubtful that it is the entire, explanation. Blinding affects these animals so profoundly that it would not seem at all impossible that something akin to heterogeneous induction finds place in their vital economy. The experiment of revolving the field of vision along with the insect I did not perform. It would be worth while. At any rate, on the theory of shifting visual impressions I am at a loss to explain the retained compensating position exhibited by the beekiller when turned head downward. If the rotation of a beekiller around a dorsi-

¹ LOEB: Sitzungsberichte der Würzburger physikalisch-medicinischen Gesellschaft, 1888.

² A certain beetle scratched the paint from its eyes by a lively motion of the front pair of legs, using right and left alternately. To prevent this happening again, these legs were cut off at the first joint. The animal did not give any sign of recognition of the loss, but continued to move the stumps as if scratching, although they could not come near the paint. Though the second pair of legs could easily have reached the eyes, no effort was made to use them for that purpose. This observation seems in harmony with recent work of Bethe on the supposed intellectual powers of insects.

³ DELAGE: Archives de zoologie expérimentale et générale, 1887, (2), v.

ventral axis is stopped the moment the head is turned to one side, the head is not kept in this position but is brought back immediately to the normal position. If when turned head downward the animal does not recognize the changed relation to gravity, why is not the head here also brought back to the normal position? Certainly it is not merely the weight of the head which causes the motion, for the reaction fails when the eyes are painted.

SUMMARY.

1. Every form of compensatory motion known to be exhibited by vertebrates is found also in invertebrates, and not only in those which possess otocysts, as crustaceans, but also in those without, as insects. If, therefore, these motions have one common organ, that organ is not the semicircular canals nor the otocysts, nor a union of these. It will be argued that the compensatory motions of insects are of a different character, being done away with by blinding, while those of fishes, for example, are practically independent of the sense of sight. I cannot do more than call attention to v. Cyon's observation that those of a vertebrate — the frog — are also dependent upon sight.

2. In the flounder, an animal in which a very great shifting of the eyes has taken place, and which has come to lie on one side so that the canals are turned 90° from their ordinary position, the regular compensatory motions of the eyes are present. The removal of a part of the canals, for example the vertical canals, has in several cases failed to eliminate compensatory motions in the plane of the extirpated canals. In one case removal of all canals left a large amount of compensatory motion. Removal of the horizontal canals in a dogfish did not eliminate compensatory motions in that plane. Removal of the otoliths from the flounder (even with the addition of blinding) did not eliminate the power of retaining compensating positions when the orientation of the animal with respect to the force of gravity was changed.

3. The (morphologically) horizontal or external canals in flounders and dogfish are far more sensitive than the vertical canals. Stimulation of a horizontal canal leads inevitably to motion of the eyes in the plane of the canal. Stimulation of a vertical canal seldom or never leads to definite motion of the eyes in the plane of the canal. Yet compensatory motions in the planes of the vertical canals are normally more active than in the plane of the horizontal. It is supposable that the connection of the horizontal canals with that part of

the motor mechanism which mediates motions in the plane of these canals is of no significance, and that while artificial stimulation of these canals causes these motions the latter normally arise from some other source.

4. Independent of the shifting of retinal impressions the compensatory motions of the eyes of crayfish are greater in the light than in the dark. The failure of such reactions in blinded insects is perhaps explainable on some such basis.

5. It is the rays of greater refrangibility which thus affect the motion of the eyestalks of the crayfish.

6. Even after both blinding and extirpation of the otocysts, crayfish continue to show a small turning of the eyes on passive rotation of their bodies in vertical planes.

I desire to thank Professor Loeb for suggestions in planning lines of work, and for ever-ready help in overcoming experimental difficulties.



